

SOME ABERRANT EXOSKELETONS FROM FOSSIL AND LIVING ARTHROPODS

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Aberrant exoskeletons of the Recent xiphosuran *Limulus polyphemus* from New York and the spanner crab *Ranina ranina* from Moreton Bay, Queensland are described. Aberrant exoskeletons are described in several trilobites, namely, the Devonian scutelluid *Spiniscutellum umbelliferum* from Czechoslovakia, the Middle Cambrian eodiscoid *Pagetia silicunda* from western New South Wales, the Middle Cambrian proasaphiscids *Maotunia distincta* and *Eymekops hermius* from northeastern China, the Middle Cambrian mapaniid *Mapania striata* from northeastern China, and the Middle Cambrian ptychoparioid *Papyriaspis lanceola* from northwestern Queensland. Possible causes of the abnormalities are discussed and an attempt made to categorize these specimens with previously described abnormalities. A specimen of the dalmanitid trilobite *Odontochile formosa* with a starfish on its pygidium and posterior part of its thorax is illustrated as a possible example of a predator at work near the Silurian-Devonian boundary.

□ Trilobita, Crustacea, Xiphosura, abnormal exoskeletons.

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Abnormalities in trilobite exoskeletons have been attributed to developmental malfunction, parasitism, or injury. A wide range of subcategories may be defined (e.g. Snajdr, 1978) but these remain the central causes. The degree of abnormality varies considerably; it may cause death, may disappear through a series of moults if inflicted on a juvenile individual, or, in the case of parasitism, may increase with growth. Recognition of the causes is not always simple and it is hoped that closer comparisons with abnormal arthropods living today may provide uniformitarian bases for identifying some causes although Conway Morris and Jenkins (1985) expressed reservations about such an approach. An extensive literature has developed on the subject (listed Boucot, 1981; see also Rudkin, 1985, Conway Morris, 1981) but documentation of further examples will add to understanding of life histories and palaeoecology. Several examples of observed or potential abnormalities in trilobites and in Recent Crustacea and Xiphosura are here described and their causes discussed.

Specimens are housed in the Palaeontology Collections of the Queensland Museum (prefix QMF), Museum of Victoria (NMVP), Department of Geology, Australian National University (ANU), Australian Museum, Sydney (AMF), and the Smithsonian Institution (USNM) and in the Crustacea Collection of the Queensland Museum (QMW).

Limulus polyphemus (Linnaeus, 1758) (Fig. 1)

A moulted but articulated carapace from the shore of Flax Pond at Stony Brook on the north shore of Long Island, New York shows major distortion to the left side of the cephalothorax anteriorly and to the left side of the abdomen. On the cephalothorax the distortion takes the form of a strong buckling of the margin with consequent buckling and twisting of the inner ridge of the doublure. This buckling has not prevented the exoskeleton splitting during moulting along the usual line, just ventral to the margin. The deformity extends to the midline around the anterior median process. On the abdomen, the distortion is in the number of marginal spines (5 on the left; 7 on the right) but otherwise bilateral symmetry appears to be intact.

Both these distortions may have been caused by mechanical deformation of the animal immediately after an earlier (probably very early) moult, while the shell was still soft. The cephalothorax may have recovered some of its original shape during subsequent moults but its departure from the normal is still marked. The original damage to the abdomen may have been to cells involved in developing the lateral spines. Whereas the shape of the abdomen returned almost to normal with growth the damaged cells resulted in loss of capacity to generate some of the lateral spines and those that were produced are smaller than usual.

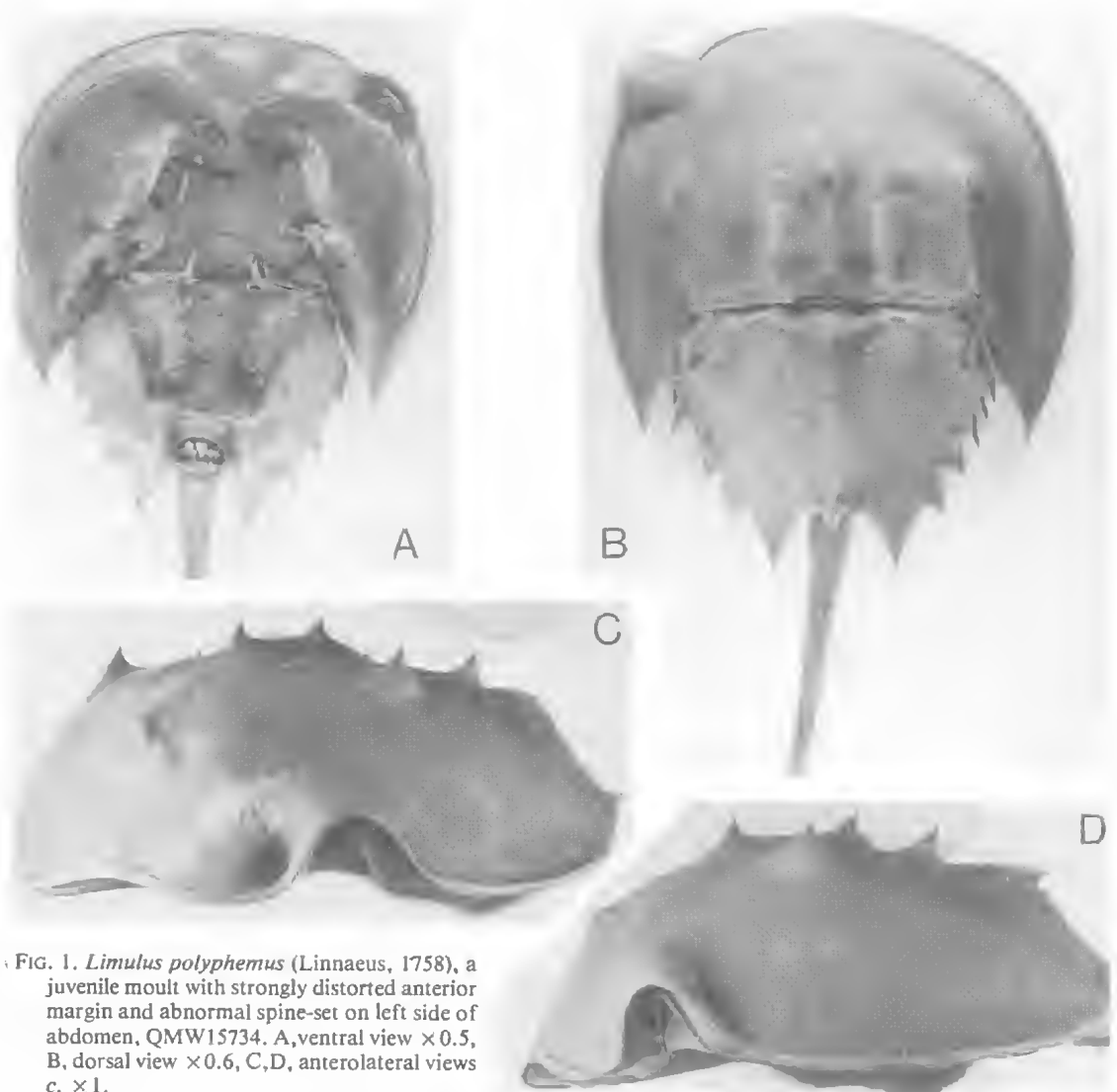


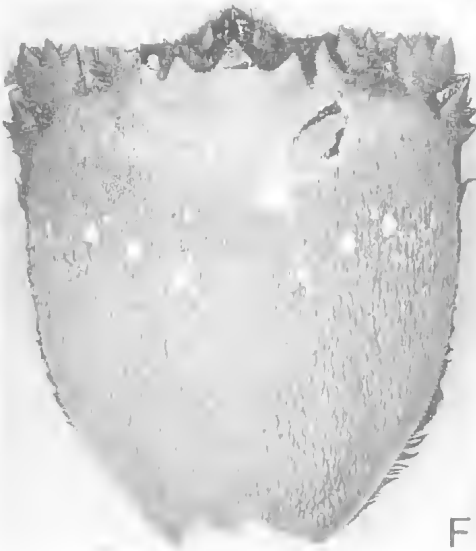
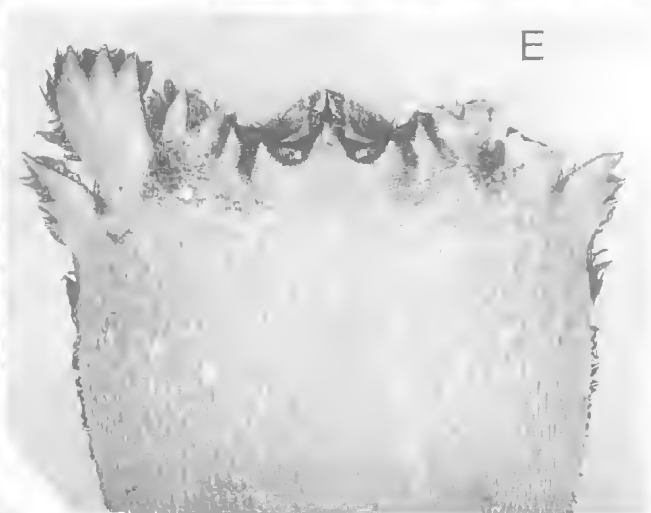
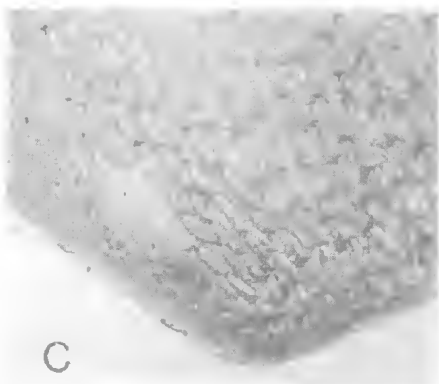
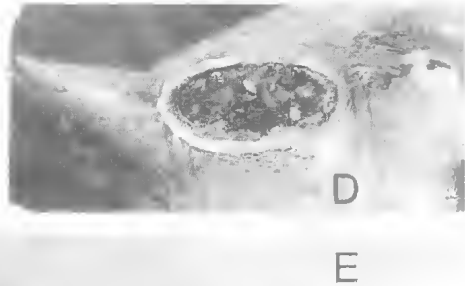
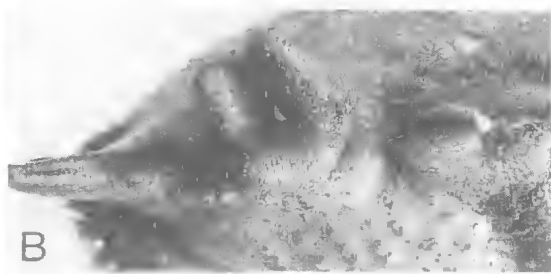
FIG. 1. *Limulus polyphemus* (Linnaeus, 1758), a juvenile moult with strongly distorted anterior margin and abnormal spine-set on left side of abdomen, QMW15734. A, ventral view $\times 0.5$, B, dorsal view $\times 0.6$, C, D, anterolateral views c. $\times 1$.

Since none of the margin was lost in the damage it is unlikely that a predator was involved. It seems likely that this sort of deformity could be caused by mechanical damage to the animal, e.g., by the animal being washed against rocks by wave action or by storm activity.

***Ranina ranina* Linnaeus, 1758**
(Fig. 2)

Carapaces of spanner crabs from Moreton Bay exhibit broken or lost spines on the anterior margin, and piercement of the carapace away from the margin are common with or without healing of the wound. Spanner crabs are taken commercially in considerable numbers (of the order of 30-40 per m^2) generally in 30-40m depths and generally without any other large species associated so I suggest that most of the injuries are

FIG. 2. *Ranina ranina* Linnaeus, 1758. A-C, carapace showing damaged right lateral process subsequently healed (B), and rounded bulge posteriorly (C), QMW15735, $\times 0.5$, $\times 2$, and $\times 1$, respectively. D, E, carapace with largest projection on right side broken off (E), and black tissue produced in fracture (D), QMW15736, $\times 0.65$, and $\times 2$, respectively. F, G, carapace in dorsal (F), and ventral (G) views, showing piercement of shell and subsequent initial stage of repair inside, QMW15737, $\times 0.5$, and $\times 2$, respectively.



inflicted by other members of the same species. To my knowledge injury of one individual by another has not been observed but I can see no other reasonable explanation. One specimen (Fig. 2A,C) also shows a local bulge posteromedially to the left of the midline, the bulge retaining the external ornament but being smooth on the inside.

The latter feature may have resulted from the carapace growing over a parasite beneath the epiderm. This bulge is akin to that seen in free cheeks of *Paradoxides oelandicus* (Westergård, 1936, fig. 8) and *P. sjogreni* (Westergård, 1936, pl.10). These fossil examples are flatter and smaller probably representing a different parasite group.

Fractures of the exoskeleton or removal of whole or partial spines in *R. ranina* show clearly the steps in wound repair outlined by J.R. Stevenson (1985, p. 31) where the break blackens due to melanin (Fig. 2D), epidermal cells form a layer of cells under the blackened membrane and the new shell covers the break on the inside (Fig. 2G). Subsequent moults lose the black layer and new shell, albeit quite deformed, is deposited over the wound (Fig. 2B).

This type of repair observed in living crustacean species may be the same as that in trilobites such as the *Mapania striata* specimen described above or the specimens of *Oxygopsis klotzi* (Rudkin, 1979), *Radioscutellum intermixtum* (Petr, 1983) or *Ceraurinaella* sp. nov. (Ludvigsen, 1977). Only the last example shows the same early stage of damage as the specimen in Fig. 2F,G. Moreover, these injured spanner crabs suggest that within trilobite communities, injuries may have been caused by one individual upon another although the walking legs of trilobites, as far as we know them, may not have been as effective weapons as chelae are on crabs. Such damage may not always be due to predation but may be due to competition within a species.

***Spiniscutellum umbelliferum* (Beyrich, 1845)
(Fig. 3)**

This large pygidium of the Family Scutelluidae from the Devonian Lochkov Shale in Czechoslovakia, has a large indentation in the lateral margin, disrupting pleural ribs and furrows. It may be significant that the second pleural rib is curved adaxially near its outer extremity so as almost to enclose the end of the third rib. The third rib is cut off and the fourth is damaged adaxial to the inner edge of the doublure with the damaged area extending more than a centimetre from the damaged margin.



FIG. 3. *Spiniscutellum umbelliferum* (Beyrich, 1845), a large pygidium with abnormal lefthand marginal area, NMVP63735, $\times 2$.

The origin of this abnormality is not clear. The standard explanations are an encounter with a predator, a mechanical accident such as being rolled around in a storm or being crushed by a heavily armoured animal or a rock. If one of these were the cause then a considerable amount of regeneration has taken place as a large part of the wound has grown over. Regeneration is suggested in the related scutelluid *Radioscutellum intermixtum* illustrated by Petr (1983). His dorsal external mould of the pygidium shows no deformation of the pleural ribs which run up to the ragged margin of the damage and no damage away from the margin. This evidence suggests that the specimen was damaged mechanically by a predator or other agency that took out cleanly a part of the exoskeleton and the damage is thus pathological rather than teratological as suggested by Petr.

My preferred explanation for the abnormality of NMVP63735 is that during moulting a part of the pygidium between dorsal exoskeleton and doublure failed to separate readily from the exoskeleton. This is a possibility in forms such as *S. umbelliferum* with wide doublures situated close to the dorsal exoskeleton. Having released from

most of its shell the animal may be trapped and begin to panic with pain from the struggle. Vigorous activity to be free of the shell may well have torn away a patch of the soft tissue with the shell. In this frenzy the animal would still try to pull soft parts out of the thin space above the doublure towards the axis. As this would have been done while the body was without a hard shell the outer margin of the soft body may have been drawn towards the axis, causing an embayment and curving the anterior pleurae. This deformity may then have been incorporated into the newly hardening exoskeleton. Accordingly I suggest that the abnormality in NMVP63735 was due to malfunction in the process of ecdysis in the centrally deformed part of the abnormality.

Pagetia silicunda Jell, 1975
(Fig. 4)

Among a large population of this early Middle Cambrian eodiscoid from the Coonigan Formation in western New South Wales, a cranidium (Fig. 4A,B) shows a cranial spine broken off near its base and grown over. Another specimen (Fig. 4C) with fully developed spine illustrates the extent of modification. Although mechanical damage cannot be ruled out it seems unlikely in such a small, planktonic species. The confined space within the cranial spine would have been tight for retraction of the soft tissue

during moulting and imperfection in release of the old exoskeleton may have induced the animal to tear off the soft tissue to be free of the molted exoskeleton. The exoskeleton subsequently laid down would lack the extension of the spine and cover the torn area as the wound healed.

A pygidium (Fig. 4D) of the same species was interpreted (Jell, 1975, p.25) as a pathological specimen deformed by a disease or a parasite. This interpretation was based on the fact that the margin intact and the deformity in the left pleura and axis is entirely divorced from the margin. Similar (i.e. isolated from the margin) abnormalities in pygidial symmetry have been accorded differing origins by (Rudkin, 1985, figs 1C, 2). In *Pseudogygites latimarginatus* (Hall, 1847) Rudkin suggested that such a 'point wound' may have been inflicted by a co-occurring nautiloid whereas in *Proetus macrocephalus* (Hall, 1888) the less localized deformity was attributed to major developmental malfunction. In the pygidium of *P. silicunda* the latter cause would seem most probable but the way in which this might have happened and the effect on the animal are not clear.

Maotunia distincta (Resser and Endo, 1937)
(Fig. 5A)

Among a large number of specimens of this proasaphiscid from the *Crepicephalina* Zone, Changhia Formation on Changxingdao Island, Liaoning this cranidium has an aberrant bulge in the anterior border furrow on the left hand side. This bulge is low, smooth, imperforate, elongate in the direction of the furrow and with irregular outline including low ridges that appear to continue into the major caecal trunk (i.e. the expression in the exoskeleton of a major blood vessel adpressed on the inner surface and attributed a secondary respiratory function (Jell, 1978)) in the border furrow and forward into the border. This bulge resembles those on European paradoxidids (Snajdr, 1978, pls 7,8) except that it does not exhibit a central perforation and apparently bears some relationship to the caecal system. It is identical to those on a pygidium of *Eymekops hermias* described below from the same locality and horizon.

These bulges on the Chinese specimens probably resulted from the activity of a parasite, the nature of which is uncertain. If it was an ectoparasite then it must have attached to the animal immediately after a moult so that the exoskeleton has grown over it and been deformed. It is also possible that this feature resulted from a diseased caecum or an

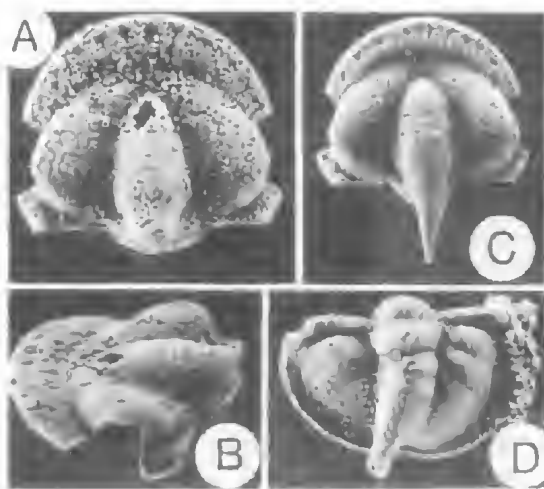


FIG. 4. *Pagetia silicunda* Jell, 1975. A,B, dorsal and lateral views of cranidium with broken but healed occipital spine, ANU27937, $\times 15$. C, undamaged holotype cranidium, ANU27797, $\times 12$. D, pygidium with abnormal left pleura and axis, AMF54980, $\times 15$.

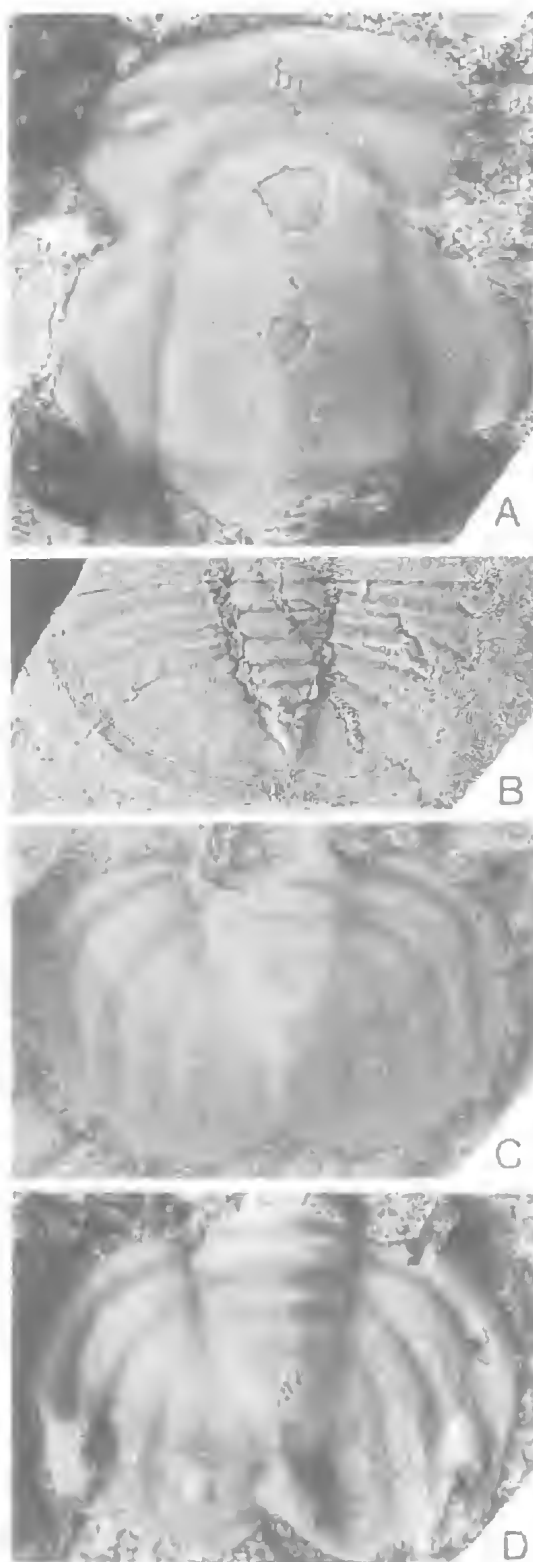


FIG. 5. A, *Maotunia distincta* (Resser and Endo, 1937), cranium showing caecum with aberrant bulge on left in anterior border furrow, USNM258672, $\times 5$. B, *Mapania striata* Resser and Endo in Kobayashi, 1935, flattened pygidium in shale with damaged right pleural area, USNM258776, $\times 3$. C, D, *Eymekops hermius* (Walcott, 1911), pygidia without (C) and with (D) abnormal bulges posteriorly, USNM258702 and USNM258699, respectively, $\times 10$.

endoparasite in the caecum as suggested by the fact that the 5 examples available all appear to be associated with the caecal system. This is in contrast to those nodes interpreted by Snajdr (1978) as of parasitic origin; their random distribution and circular shape suggest that they were caused by ectoparasites and their common occurrence in the protective hollows of pleural furrows supports this view. It is not possible to tell whether the abnormalities result from a disease in the structure forcing the exoskeleton to grow into a bulge to accommodate it, or whether they are the result of endoparasites lodged in that respiratory system causing enlargement of the caecum and bulging of the exoskeleton around it. At present I would suggest the latter only because I would expect abnormalities in development to be more elongate.

Eymekops hermius (Walcott, 1911)
(Fig. 5C,D)

On a pygidium (Fig. 5D) 4 large bulges (or nodes, in Snajdr's (1978) terminology) and numerous enlarged caeca across the posterior are of irregular shape, smooth, and appear to extend outwards as low ridges into the caecal network. By comparison with other pygidia of this species (Fig. 5C) these bulges are aberrant. Although 2 of the large bulges (one at posterior of axis and one on far left) appear to have small perforations close examination shows these to be irregular around their margins and therefore almost certainly the result of damage to the specimen during or after collection. These bulges are judged to be caused by an agent similar to that which affected the cranium of *Maotunia distincta* described above. Speculation on the cause is detailed under that species above.

Mapania striata Resser and Endo, 1935
(Fig. 5B)

A pygidium crushed in shale of the Changhia Formation (*Amphoton* Zone) on Changxingdao Island, Liaoning has part of its right pleural area missing. There is a ragged edge to the pleural area over the anterior 4 segments of the pygidium. The

doublure is removed although an extremely narrow doublure appears to have regrown on the 2 anterior segments. There appears to be little distortion of the exoskeleton adjacent to the missing parts; the most logical conclusion is that a part of the pleural field was actually removed probably by the bite of an unknown predator or less likely by a pure accident. Healing of the injury in the form of growing a new doublure puts this specimen in the same class as those described by Rudkin (1979) of *Ogygopsis klotzi*. I agree with Rudkin's interpretation of such injuries. No large predator capable of inflicting such a wound is known from the Middle Cambrian of north China.

***Papyriaspis lanceola* Whitehouse, 1939**
(Fig. 6)

One specimen lacking the cephalon, from the Middle Cambrian V Creek limestone of *Ptychagnostus punctuosus* Zone age on the Camooweal to Burketown road at the crossing of V Creek shows two types of distortion not seen on the immediately adjacent specimen of the same species. On the left side, the last 3 thoracic segments are strongly embayed with callous development around the margin of the embayment. This embayment is similar to that on *Olenellus robustus* (Burling) (Rudkin, 1979, fig 2B) and to those in *Ogygopsis klotzi* (Rudkin, 1979, fig. 1).

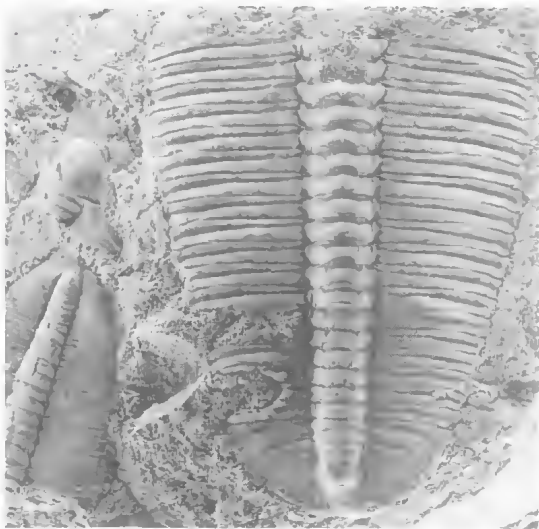


FIG. 6. *Papyriaspis lanceola* Whitehouse, 1936, large thorax and pygidium with last 4 segments abnormal on both sides (small normal thorax and pygidium on same slab with cranidium of *Maotunia angusta* (Whitehouse, 1939) as well) QMF17442, $\times 1$.

It is well healed and so the animal has completed at least one moult after the damage occurred. The original outline of the damage may not have been so well rounded. As this species had a very thin shell (Jell, 1978) the damage may have been caused by some agency that was not particularly violent e.g. some other trilobite of heavier build may have torn the exoskeleton and tissue with a genal or pygidial spine during either chance encounter, mating or assault.

On the right side the 4 posterior thoracic segments each exhibit an irregular node in different places, without obvious damage to the margin. Whereas these nodes could be classified with those described by Snajdr (1978) as of parasitic origin on paradoxidids, I suggest they more probably resulted from damage to the exoskeleton caused during the same incident that damaged the left side. With at least one subsequent moult, the damage has been almost obliterated by growth of the new exoskeleton leaving only these nodes which resemble those near the margin on the left side. The cause of these nodes is equivocal showing how difficult interpretation is in these cases.

***Odontochile formosa* Gill, 1948**
(Fig. 7)

Mainly because of their habit today most starfish have long been reputed to be predatory in the Palaeozoic, though little fossil evidence has ever been brought to light to support this contention. The present specimen comes from the Clonbinane Sandstone Member (Ludlow) of the Humevale Formation at Museum of Victoria fossil locality NMVPL300 in the vicinity of an old mine on Comet Creek, c. 4.6km southeast of Clonbinane, central Victoria. Hundreds of complete starfish and brittlestars, articulated brachiopods and whole trilobites are known from the same locality. I interpret this fauna as probably displaced by catastrophic sediment movement and buried alive. Therefore the association illustrated, of a complete trilobite and starfish, may be fortuitous but it is more likely that the starfish is attacking the trilobite because so much of the starfish is in direct contact with the trilobite exoskeleton. Damage to the exoskeleton is not certain but the arm of the starfish pointing to the posterior of the trilobite appears to be where the exoskeleton should be, and may indicate that part of the exoskeleton had been removed already.

Although it is difficult to be certain of the interpretation of associated fossils this example appears

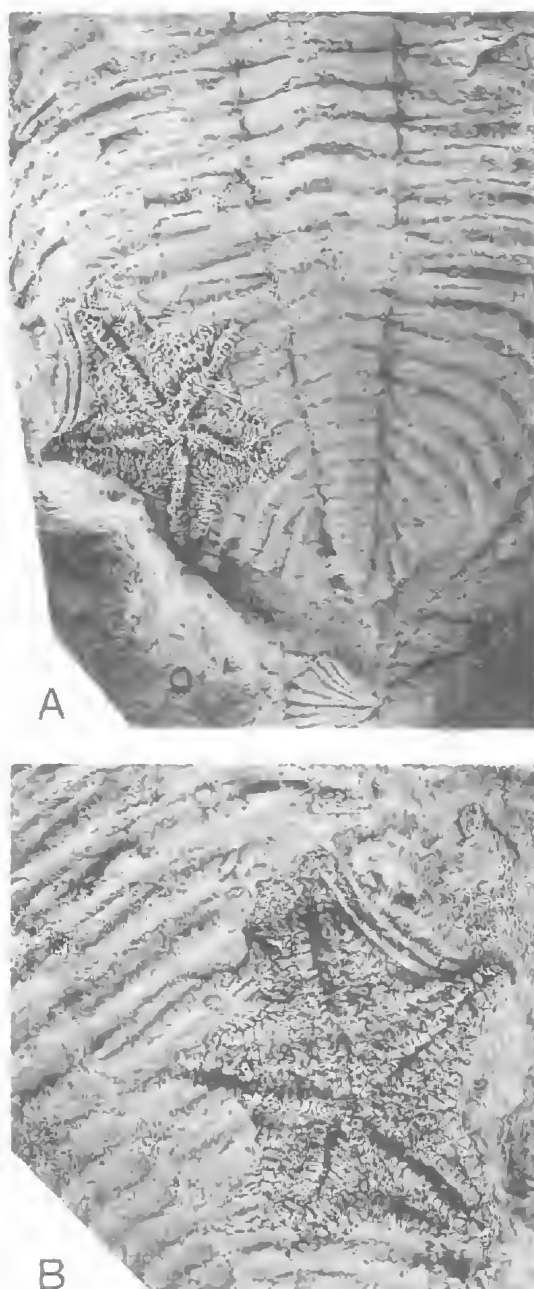


FIG. 7. *Odontochile formosa* Gill, 1948, a large thorax and pygidium with a relatively small, undescribed starfish resting on the pygidium, NMVP113343, $\times 0.5$. A, internal mould of ventral (or oral) surface of starfish and of dorsal surface of trilobite; posterior arm of starfish at lower left. B, ventral view of latex cast of ventral surface of starfish (axis of trilobite pygidium along lower left diagonal of print and posterior arm of starfish in lower right).

to be one of the most direct pieces of evidence so far found for starfish acting as predators in the Palaeozoic.

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